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Life history traits of the exploited Nile Tilapia (*Oreochromis niloticus* – Cichlidae) in a subtropical reservoir (Lao PDR)

by

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Abstract. – Biological traits of *Oreochromis niloticus* were studied in order to identify potential differences between the population of the Nam Theun 2 Reservoir and other populations in Asia and in Africa. The study also aimed to characterize the demographic structure of the exploited population by fisheries in the reservoir. Toluidine-stained transverse section of otoliths from 322 specimens, collected between November 2015 and January 2017, were analysed to identify the periodicity of annulus formation and to age individuals. Length, weight, sex and sexual maturity stage were recorded. Life history traits were characterized by length-weight and length-age relationships. The periodicity of annulus formation was annual, with complete formation of the translucent zone at the beginning of the warm and wet season (June and July). The length-age key has been established and was composed of 9 age classes, ranging from 0 to 8 years old. Males showed positive allometric growth whereas juveniles and females exhibited isometric growth. The study showed an asymptotic standard length of 658 mm and a low growth rate ($K = 0.08 \text{ year}^{-1}$). The sex ratio was equilibrated, and first maturity of females was at 277 mm standard length. The population was composed of individuals aged 3 years old and older, and 60% of the landings were composed of individuals aged 5 years and older. The growth rate was lower than for Asian and African populations, and the age-length key provided was specific to the studied reservoir. However, some biological traits of the *O. niloticus* population were similar to those found for other population in the world: (i) formation of an annual annulus during the reproduction period, at the beginning of the warm and wet season like populations from subtropical countries, and (ii) an isometric or a positive allometric growth as seen in populations that were not overexploited and were living in favourable environmental conditions. Therefore, the present study suggests that the *O. niloticus* population of the NT2 Reservoir was not overexploited at the time of the survey.

Résumé. – Histoire des traits de vie du Tilapia du Nil (*Oreochromis niloticus* – Cichlidae), espèce exploitée d'un réservoir subtropical (Laos).

Les traits d'histoire de vie d'*Oreochromis niloticus* ont été étudiés afin d'identifier de potentielles différences entre la population du réservoir de Nam Theun 2 au Laos et d'autres populations asiatiques ou africaines. La caractérisation de la structure démographique des captures issues des pêches artisanales et de subsistance a aussi été réalisée. Les sections transversales d'otolithes de 322 spécimens collectés entre novembre 2015 et janvier 2017 ont été analysées pour identifier la périodicité de formation de l'annulus et déterminer l'âge des individus. La taille standard, le poids, le sexe et le stade de maturité des gonades ont parallèlement été collectés. Les relations taille-poids et taille-âge ont été caractérisées. Les résultats ont indiqué qu'un annulus se formait par an avec une zone translucide totalement formée au début de la saison des pluies (juin-juillet). La clé taille-âge a été établie et comprend 9 classes d'âge allant de 0⁺ à 8⁺ ans. Les mâles présentaient une allométrie positive et les juvéniles/femelles une isométrie. La taille asymptotique a été estimée à 658 mm et le taux de croissance à 0.08 an^{-1} . Le sexe ratio était à l'équilibre et la première maturité sexuelle des femelles a été estimée atteinte pour une taille standard de 277 mm. La part de la population exploitée était composée d'individus âgés de 3 ans et plus, et 60% des débarquements étaient composés d'individus de 5 ans et plus. Le taux de croissance s'est révélé bien plus faible pour cette population que pour les autres populations d'Asie et d'Afrique, induisant une clé taille-âge spécifique à la population du réservoir. Cependant, certains traits biologiques ont montré des similarités avec les autres populations. Ainsi comme les populations des pays subtropicaux, la population du réservoir a montré la formation d'un annulus par an lors de la période de reproduction de l'espèce. Les relations allométriques se sont aussi avérées similaires à celles trouvées pour les populations non-surexploitées des autres pays et vivant dans des écosystèmes présentant des conditions environnementales favorables. Cette étude a aussi permis de conclure que la population du réservoir de Nam Theun 2 n'était pas surexploitée au moment du suivi.

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The Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758), a benthopelagic fish species of the Cichlidae family, is an ubiquitous freshwater species. Southern Egypt, tropical and subtropical African countries, from east to west, and Israel and Jordan in the Middle East, are known to be the native biogeographic range of this species (Pullin *et al.*, 1997; Ishikawa *et al.*, 2013). Currently, this species is widely distributed throughout the world, due to its introduction in many countries after 1945 to control aquatic vegetation, to use as bait fish or to develop aquaculture (Costa-Pierce, 2003; Canonico *et al.*, 2005). *O. niloticus* was introduced in Southeast Asia, such as in Thailand, in the mid-1960s for aquaculture purposes (Pullin *et al.*, 1997; De Silva *et al.*, 2004). The species was later promoted for aquaculture development in the early 1990s in Lao People's Democratic Republic (PDR) (Garaway *et al.*, 2001). In Lao PDR, like in other countries, this exotic species is well established due to its self-reproduction (De Silva *et al.*, 2004; CABI, 2018) facilitated by its particular life history traits and plasticity (Ishikawa *et al.*, 2013). These characteristics enable it to be a pioneer species that can thrive in various ecosystems such as lakes, estuaries and rivers (Njiru *et al.*, 2006; Ishikawa *et al.*, 2013), and even disturbed ecosystems such as reservoirs (Gómez-Márquez *et al.*, 2008; Novaes and Carvalho, 2012). In Lao PDR, this exotic fish species occurs in various freshwater ecosystems of the Mekong Basin, such as the tributaries, wetlands, and some hydropower reservoirs (Kottelat, 2001).

In Lao PDR, a landlocked country, freshwater ecosystems have a major impact on the local population's economy. In addition to rice farming and animal husbandry, fishing by households is recognized to be important for food security. The principal source of protein for Laotians comes from local freshwater fish. Among the various freshwater ecosystems present in this country, hydropower reservoirs contribute significantly to local production and income generation (FAO, 2006). Phonvisay (2013) indicated that 40% of the fish production in Lao PDR came from reservoirs. This production can be expected to be stable or even increased since a 2013 assessment indicated that 17 hydroelectric reservoirs were operational and 14 were under construction (Mottet and Lasserre, 2014). *O. niloticus* tends to dominate the landings in Asian reservoirs, especially when stocking programmes are performed with this exotic species (Amarasinghe and De Silva, 2015). Despite the increasing number of reservoirs, the contribution of the species to the landings for Lao reservoirs is poorly documented (Cottet and Visser, 2017). The Nam Theun 2 Reservoir (NT2), the second largest reservoir in Lao PDR, implemented fishery monitoring, including species contribution in landing sites following the different ecological phases of the reservoir following the impoundment (Cottet *et al.*, 2016; Cottet and Visser, 2017). These phases are a trophic upsurge, followed by a trophic depletion and

then a stable production. The catches of *O. niloticus* encompass 52% of the landings since the NT2 Reservoir has started to reach its stabilization phase in 2012 (Cottet and Visser, 2017).

In the context of exploited species management and sustainable fishery management, the knowledge of biological traits of exploited fish species, such as age, age/size at maturation and growth, are relevant information to identify the potential over-exploitation of a species (Devries and Frie, 1996; Bezerra-Neto *et al.*, 2012). The biological traits of *O. niloticus* are well documented in Africa (*e.g.* Duponchelle and Panfili, 1998; Admassu and Casselman, 2000; Bwanika *et al.*, 2007; Ouattara *et al.*, 2009; Yongo and Outa, 2016), and also, but to a lesser extent, in areas where the species has been introduced, for example in America (*e.g.* Peterson *et al.*, 2004; Gómez-Márquez *et al.*, 2008; Novaes and Carvalho, 2012) and in some Asian countries (*e.g.* Amarasinghe, 1987; Chapman and Fernando, 1994; Ishikawa *et al.*, 2013). Age and growth of *O. niloticus* distributed in Lao reservoirs remain unknown, although these biological traits can change in response (i) to environmental factors (*e.g.* temperature, food availability, parasitism (Wootton, 1990)) and/or (ii) to anthropic pressures (*e.g.* fishing pressure, pollution (Sparre and Venema, 1996; Helfman *et al.*, 2007)).

In this context, the objective of this study was to provide data on life history traits of *O. niloticus* in the NT2 Reservoir system by obtaining (i) demographic data using age estimation, and (ii) growth parameters using individual age estimation from otoliths and length-at-age structures. The results were compared with those available from other reservoirs and ecosystems in Asia and Africa to identify potential differences in biological traits. Furthermore, the established age-length key would allow (i) the characterization of the demographic structure of the exploited stock, and (ii) to answer questions regarding sustainability of the *O. niloticus* fishery in the NT2 Reservoir.

MATERIALS AND METHODS

Study site

The NT2 Reservoir is located in the centre of Lao PDR (Khammouane Province, 17°N and 105-104°E, Fig. 1), on the Nakai Plateau, approximately 538 m above sea level at the full supply level (Descloux *et al.*, 2011). Its impoundment lasted from April 2008 to February 2009, and its exploitation started in April 2010 (Descloux and Cottet, 2016). The subtropical NT2 Reservoir experiences a monsoon regime. The warm and wet season (WW) is from June to October, the cold and dry season (CD) is from November to February and the warm and dry season (WD) is from March to May (Descloux and Cottet, 2016). The reservoir surface varies between 489 km², at its maximum level at the beginning of the CD sea-

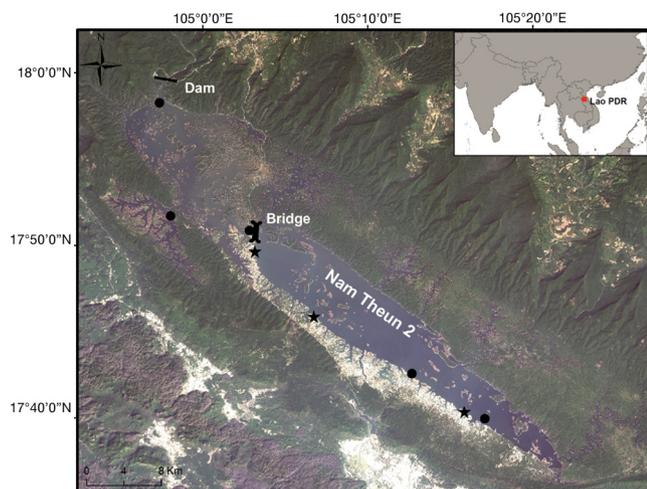


Figure 1. – Map of the Nam Theun 2 Reservoir in Lao PDR at its higher level (538 m a.s.l) and localization of sampling sites (black dots) by experimental gillnet fishing and of villages (black stars) for the monitoring of landing/fishing effort.

son in November, to 86 km² at the end of the WD season in June (Chanudet *et al.*, 2015). The NT2 Reservoir is dendritic, with a mean depth of 11 m and a maximum depth of approximately 38 m near the dam (Martinet *et al.*, 2016). The water surface temperature varies from approximately 18°C at the end of the CD season to approximately 32°C at the end of the WD season (Chanudet *et al.*, 2015). The reservoir was classified as meso-oligotrophic between 2008 and 2011 (trophic upsurge period) and has evolved since 2011 to an oligotrophic status (Descoux and Cottet, 2016; Martinet *et al.*, 2016). Sixteen resettlement hamlets are located along the southwestern coastline and composed of approximately 2182 households in 2014, and 85% of households practise fishing activities for subsistence and income generation (Cottet and Visser, 2017). Fisheries in the NT2 Reservoir are composed of multiple fish species. However, the contribution of the catch underlined the dominance of *O. niloticus*, which reaches more than 50% of the total catch in the stable phase (Cottet and Visser, 2017). During the impoundment, some aquaculture ponds were inundated, and some individuals of *O. niloticus* could have established in the NT2 Reservoir.

Fish sampling

Oreochromis niloticus specimens were collected monthly between November 2015 and January 2017 from various sites on the NT2 Reservoir using gillnets (Fig. 1). The mesh sizes were 10, 15, 20, 25, 30, 35, 40, 50, 60 and 70 mm between knots (Cottet *et al.*, 2016). Some additional specimens were collected from fishermen (large individuals: standard length greater than 250 mm), and by using a push net (mesh size 2 mm) in various reservoir swamps (to capture juveniles) to complete the size range and refine the analysis.

All the collected specimens were sacrificed. Standard length (SL) and total length (TL) were recorded to the nearest mm, and total weight (W) was recorded to the nearest 0.1 g. The specimens were sexed (juvenile, female, male and undetermined) by macroscopic examination of gonads. The “undetermined” term was attributed when the decomposition status of the specimen did not allow the determination of sex by macroscopic examination of gonads. Furthermore, the maturation status was defined for male and female according to the scale described by Pilling *et al.* (2007). Sagittal otoliths were removed, cleaned and stored dry until further examination.

Otolith preparation

Right otoliths were embedded in polyester resin (SODY 33 with its catalyst) and sectioned transversely through the core using precision micro-cutting (ISOMET Buehler Low Speed Saw 11-1180-250) with a diamond disc cutter of 0.38 mm thickness. The sections were sanded manually first using a 1200- μ m abrasive disc and then using a 2400- μ m disc in order to reach the core as mentioned by Panfili *et al.* (2002). Afterward, they were polished using a felt disc with a suspension alumina solution of 1 μ m. The sections were etched for 5 minutes with a 5% Ethylene-Diamine-Tetraacetic Acid (EDTA) solution (Panfili *et al.*, 2002). This step partially demineralizes the otolith, and the highly mineralized and more organic regions become clearly distinguishable (Panfili *et al.*, 2002). The sections were stained for 7 minutes with 1% toluidine. The translucent zone, characterized by slow growth, is stainable by toluidine blue and is also named translucent chromophilic zone after the coloration step (Panfili *et al.*, 2002). All sections were examined under a binocular loupe (Olympus SZ40) under reflected light, using a camera (Olympus SC50 and a SZ CT V camera rack, CellSensEntry software).

Age estimation and validation

The type of zone (translucent or opaque) on the otolith edge was identified macroscopically, and the translucent stained zones were counted along the ventral axis of the otolith (Fig. 2). Counts for each section were performed twice by the same reader with an interval of 2 weeks, without knowledge of the fish length. To estimate ageing precision, the percentage of full agreement, the coefficient of variation (CV) and the average percentage of error (APE) between readings were calculated (Campana, 2001). Otoliths presenting vateritic growth and indistinct annulus character were excluded from the analysis. The individual age was calculated using the capture date, the mean birth date (assumed to be 1 June, due to a peak of reproduction observed in May for the *O. niloticus* population in the NT2 Reservoir), and the otolith edge aspect (stained or not) (Morales-Nin and Panfili, 2002).

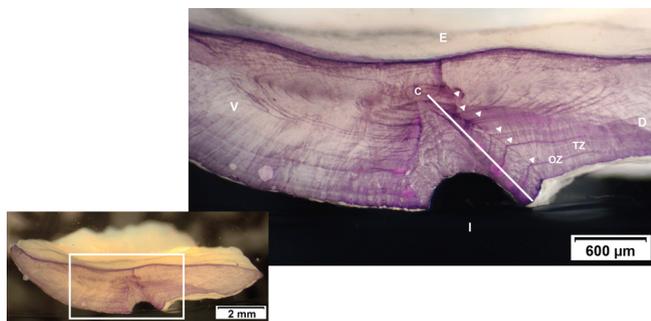


Figure 2. – Transverse section of otolith (sagittae) from a 6+ year-old *Oreochromis niloticus* from the Nam Theun 2 Reservoir in Lao PDR. The section was stained with toluidine blue and viewed using reflected light: the coloured translucent zones are counted along the sulcus axis. Core (C), translucent stainable zone (TZ), opaque zone (OZ), ventral face (V), dorsal face (D), external face (E), and internal face (I).

The age-length key was determined to examine whether the ages of fish could be reliably estimated from their lengths. To be able to make comparisons with previous studies of *O. niloticus* (Duponchelle and Panfili, 1998; Gómez-Márquez, 1998; Ishikawa *et al.*, 2013) age-length data were grouped into 20-mm length classes.

Length-weight relationship

The regression equation $W = a SL^b$ was used to describe the relationship between standard length and weight, where a is a constant and b is the growth exponent or length-weight factor. Length-weight relationship was established after a log-transformation $\text{Log}_{10} W = \text{Log}_{10} a + b \text{Log}_{10} SL$ (Beckman, 1948). Differences in the fish weight to fish length relationship between sexes were analyzed using analysis of covariance (ANCOVA) on the transformed data (Scherrer, 1984). Growth was qualified as isometric if b was equal to 3 and as allometric if b was different from 3 (Ricker, 1975). To ensure the growth characterization, Student's t -test was performed for each sex to identify whether b was significantly different from 3 (Scherrer, 1984). The statistical analyses were carried out using R software (R Development Core Team, 2009).

Growth parameters and first sexual maturity

Ages and SL were fitted to the von Bertalanffy growth function (VBGF) using the nonlinear least-squares method (Gauss-Newton) to estimate the growth parameters. The VBGF is defined by the equation: $L_t = L_\infty(1 - e^{-K(t - t_0)})$, where L_t is the length at age t (in years), L_∞ is the asymptotic length, K is the growth curvature (year^{-1}) and t_0 is the hypothetical age at zero standard length.

The sex ratio was obtained using data collected between November 2015 and January 2017 and calculated as M:F (Number of males/Number of females). The sex ratio was analyzed by Chi-square test to identify if the proportions of

males and females differed from the expected ratio (1:1).

Average length at first maturity (L_{50}) is the standard length at which 50% of the females were sexually mature. The estimation of L_{50} was realized for female. Females at stage 3 or more on the maturity scale were classified as mature. Females were grouped by size classes of 20 mm as the age-length interval. Then the relative frequency of females in reproduction activity was calculated for each size class. The SL_{50} was estimated by fitting the fraction of mature females ($\% F_{\text{mat.}}$) to a logistic function using nonlinear regressions and a least squared reduction method (the Newton method, Lowerre-Barbieri *et al.*, 1996; Duponchelle and Panfili, 1998). The SL_{50} was calculated using the following equation:

$$\% F_{\text{mat.}} = 1 / (1 + \exp(-a(SL - SL_{50})))$$

with a as a constant.

The A_{50} was calculated with the following equation:

$$\% F_{\text{mat.}} = 1 / (1 + \exp(-a(\text{Age} - A_{50})))$$

using a same least square reduction method that was used to calculate SL_{50} .

The statistical analyses were carried out using R software (R Development Core Team, 2009).

Demographic structure of exploited stock

During 2016, monitoring of landing and fishing effort were conducted monthly in three villages by the manager of the NT2 Reservoir (Fig. 1). The villages were chosen in order to cover the extent of the reservoir, knowing that the zone at the north of the Thalang Bridge does not contain any village. For the landing monitoring, each village was sampled for 5 consecutive days per month. Each day, the first 10 fishermen reaching the landing site were individually interviewed (fishing gear used, mesh size or hook numbers, fishing site, time of fishing), and catches were recorded (determination of the species, weight and standard length of individuals). In parallel, the fishing effort in these same villages was monitored. Each day, the first 20 fishermen were interviewed to determine whether they were fishing or not, and if they were, the same questions from landing monitoring regarding the fishing trip were asked (fishing gear used, mesh size or hook numbers, fishing site).

With these datasets, a table of the number of individuals of *O. niloticus* caught per size class (interval of 20 mm) was created. The age-length key was transformed into proportions to give the probability that a fish of a given age i had a given length j (Panfili *et al.*, 2002). Then, as described by Panfili *et al.* (2002), the vector of the fish numbers caught at a particular length was multiplied by the age-length key, and a vector of numbers caught at a particular age was obtained. As the individuals with a standard length higher than 360 mm were not present in the otolith sampling survey, they were considered as individuals belonging to age groups $> 8^+$, according to the age-length key established by otolithometry.

RESULTS

From November 2015 to January 2017, a total of 322 *Oreochromis niloticus* specimens were collected with (i) 138 from experimental fishing, (ii) 181 from fishermen and (iii) 3 from the push net. Specimens ranged from 31 to 360 mm for SL and from 1.4 to 2173 g for W (Tab. I). A male had the maximal standard length and another male the maximal weight. In total, 80.4% of the fish samples were sexed and classified as juvenile, male or female. The remaining 19.6% could not be sexed due to an advanced stage of decomposition. Of the 318 examined otoliths, only 18.6% were excluded from the age and growth analyses due to vateritic growth, deformations or indistinct annuli.

Age estimation and validation

The mean coefficient of variation (CV) and the mean percentage of error (APE) between readings presented relatively low values (1.5% and 1.1%, respectively) indicating good agreement between the two counts (92.3%).

Despite a lack of collected or interpretable specimens for the November-December 2015, February-March 2016 and December 2016 periods, it was possible to observe that the translucent zone began to be laid in May, lasted to September and reached a peak in June-July (73%, Fig. 3). The translucent zone started to appear at the end of the WD season and lasted the first half of the WW season. Only one translu-

cent zone was formed per year, and this means that counting the translucent zones could infer individual age.

Age estimation of fish ranged from 0+ to 8+ years old. Age 4+ was the most dominant group (34.9%), followed by age 5+ (29.5%) and age 3+ (18.6%) (Tab. II). The age-length key showed a range of ages for a given size. For example, specimens measuring 230 mm SL could be from 3+ to 6+ years old, although the majority (74%) were between 4+ and 5+ years (Tab. II). It also showed a range of sizes for a given age. For example, a specimen aged 5+ years could be from 100 to 319 mm, although the majority (61%) were between 200 and 259 mm.

Length-weight relationship

The length-weight relationships for *O. niloticus* (Fig. 4) differed among sex categories if the juveniles were considered (ANCOVA: slopes, $F = 36560.14$, $p < 0.001$; intercepts, $F = 8.81$, $p = 0.115$; $R^2 = 0.99$). The fitted equations were as follows:

Juveniles: $\text{Log}_{10} W = 3.0433 \text{Log}_{10} SL + 0.00002$ ($n = 34$; $R^2 = 0.993$; $p < 0.001$);

Females: $\text{Log}_{10} W = 2.8204 \text{Log}_{10} SL + 0.0001$ ($n = 118$; $R^2 = 0.932$; $p < 0.001$);

Males: $\text{Log}_{10} W = 3.1049 \text{Log}_{10} SL + 0.00002$ ($n = 105$; $R^2 = 0.986$; $p < 0.001$).

Student's t-tests indicated that the value of b was significantly different from 3 for males ($b = 3.1049$ and $p < 0.05$), indicating allometric growth. For females and juveniles, the values of b were not significantly different from 3 (2.8204 and 3.0433, respectively), indicating isometric growth.

Growth parameters and first sexual maturity

Adjustment of the von Bertalanffy growth curve from the age-standard length data for combined sexes ($n = 258$) is presented in figure 5. The estimated von Bertalanffy growth constants were: $L_{\infty} = 658$ mm,

Table I. – Standard length (mm) and weight (g) per sex for *Oreochromis niloticus* from the Nam Theun 2 Reservoir in Lao PDR, N indicates the effective sample size and SD is the standard deviation.

	Juvenile	Female	Male	Unsexed
N	36	117	106	63
Mean SL (\pm SD)	101 (\pm 55)	230 (\pm 37)	209 (\pm 62)	139 (\pm 139)
SL _{min.}	31	112	79	40
SL _{max.}	222	320	360	255
Mean W (\pm SD)	77.4 (\pm 106.1)	490.5 (\pm 224.3)	470.7 (\pm 398.5)	156.7 (\pm 156.8)
W _{min.}	1.4	47.9	12.6	2.2
W _{max.}	437.1	1310.8	2173.9	617.3

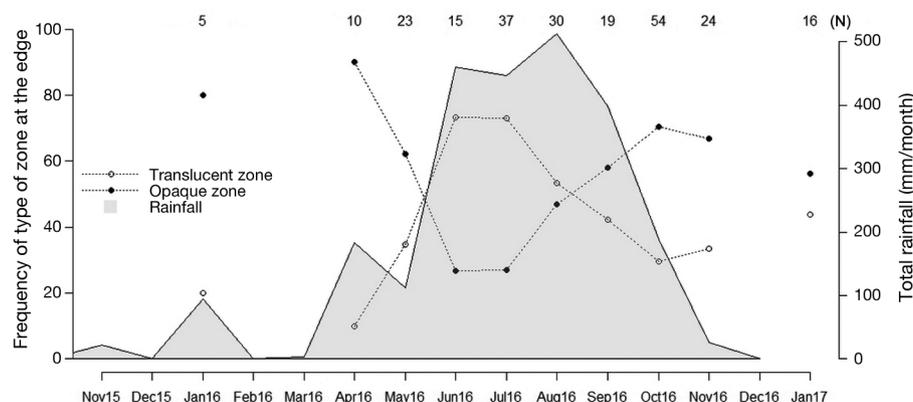


Figure 3. – Monthly frequency evolution of the translucent and opaque zones at the edge of otoliths from *Oreochromis niloticus* from the Nam Theun 2 Reservoir in Lao PDR based on transversal section readings; the number of sampled specimens is given at the top of the figure for each month (N).

Table II. – Age-length key for *Oreochromis niloticus* from the Nam Theun 2 Reservoir in Lao PDR based on transversal section readings of otoliths; sexes, including unsexed specimen, are combined; standard length (SL).

SL intervals (mm)	N	Age group (years)									
		0+	1+	2+	3+	4+	5+	6+	7+	8+	
20-39	1		1								
40-59	7	1	2	3	1						
60-79	9	2		3	4						
80-99	4			1	2	1					
100-119	8			1	1	4	2				
120-139	15		1		6	7	1				
140-159	18			2	9	6	1				
160-179	14			3	2	6	3				
180-199	21				5	10	6				
200-219	51				10	20	21				
220-239	38				7	15	13	3			
240-259	26				1	8	12	5			
260-279	19					8	8	3			
280-299	16					3	6	5	1	1	
300-319	8					1	3	4			
320-339	2					1			1		
340-359	1								1		
Total	258	3	4	13	48	90	76	20	3	1	
Percentage	100	1.2	1.6	5.0	18.6	34.9	29.5	7.8	1.2	0.4	
Mean SL		61.0	63.5	105.5	165.4	205.0	228.1	271.1	320.3	280.0	
Standard error		13.1	24.2	14.4	7.5	5.2	4.6	6.6	25.1	NA	

with the 95% confidence interval between 366 and 1472; $k = 0.08 \text{ year}^{-1}$, with the 95% confidence interval between 0.02 and 0.18, and $t_0 = -0.66$ years, with the 95% confidence interval between -1.43 and 0.07 . The value of asymptotic SL (L_∞) was higher than the maximal observed SL (360 mm).

Males comprised 44.7% ($n = 85$) and females 55.3% ($n = 105$) of the catches, with a sex-ratio (M:F) of 0.80:1. The statistical test did not indicate that the sex ratio differed significantly from 1:1 ($p = 0.1679$). The SL_{50} of females was 278 mm, and age at first sexual maturity was estimated to be 4.9 years old (Fig. 6).

Demographic structure of exploited stock

The *O. niloticus* stock exploited by the fisheries of the NT2 Reservoir between March and December 2016 was composed of individuals with an SL between 80 and 495 mm, with most individuals ranging from 200 to 300 mm, representing 71% of this landing (Fig. 7). Furthermore, the stock was composed of individuals aged 3+ years or more (Fig. 7). Individuals at 4+ years of age represented 32%, and individuals of 5+ years of age and more represented 60% of land-

ings. For the more exploited size classes, individuals aged 4 and 5 years represented 75% of landed individuals.

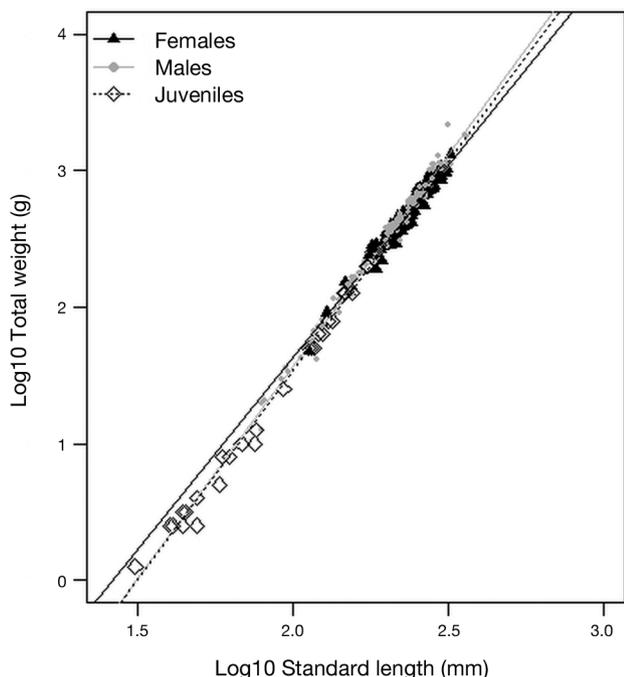


Figure 4. – Length-weight relationship of *Oreochromis niloticus* from the Nam Theun 2 Reservoir in Lao PDR between November 2015 and January 2017 according to sex.

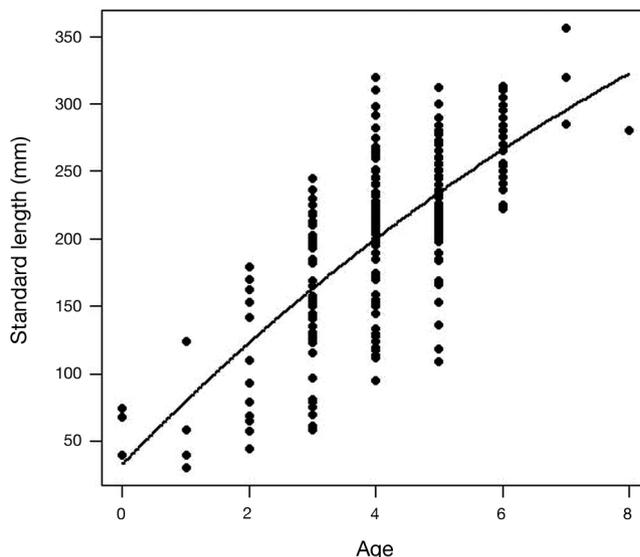


Figure 5. – Von Bertalanffy growth curve adjusted to the age-standard length of *Oreochromis niloticus* from the Nam Theun 2 Reservoir in Lao PDR between November 2015 and January 2017.

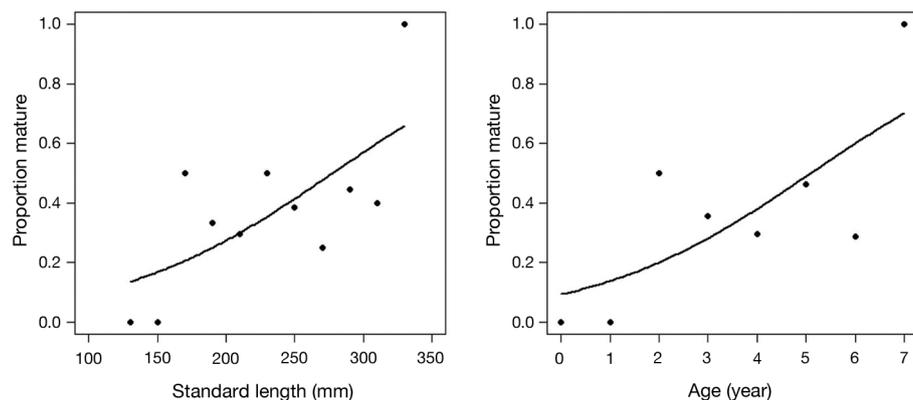


Figure 6. – At left, percentage of mature *Oreochromis niloticus* females by 20 mm standard length intervals, a fitted to logistic function from the Nam Theun 2 Reservoir in Lao PDR in 2016; at right, percentage of mature *Oreochromis niloticus* females by age (year), fitted to a logistic function from the Nam Theun 2 Reservoir in Lao PDR in 2016.

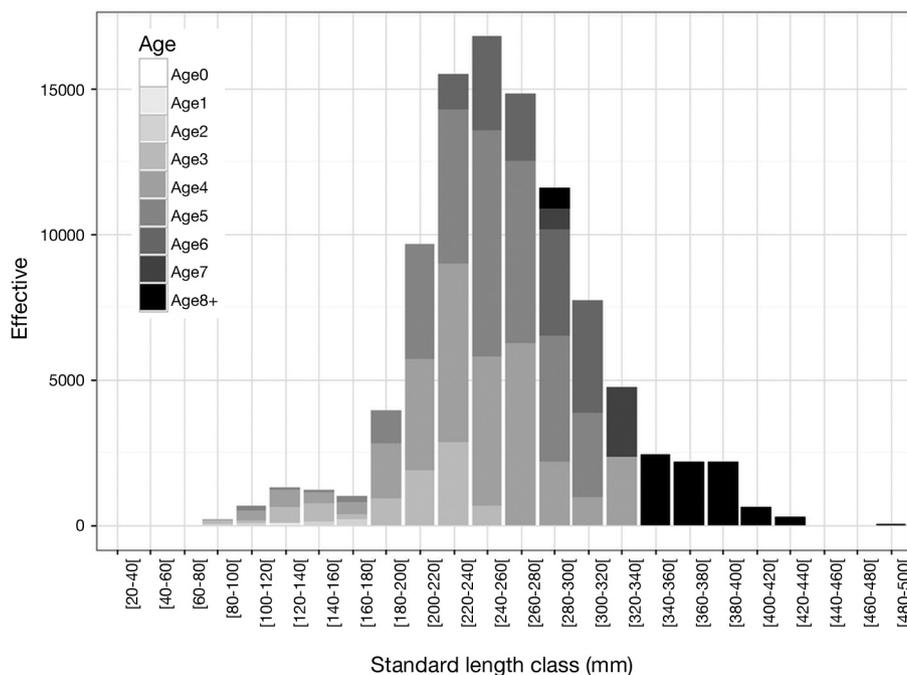


Figure 7. – Demographic structure of the exploited stock of *Oreochromis niloticus* by fisherman at the Nam Theun 2 Reservoir in Lao PDR between March and December 2016.

DISCUSSION

Investigation of life history traits of *Oreochromis niloticus* are numerous from aquaculture populations, but studies of populations living in rivers and reservoirs are fewer. This lack of data on reservoir populations needs to be remedied, especially as these ecosystems have become more abundant, notably in Southeast Asia.

Determining first the timing of increment deposition is critical for validating age estimations. Depending on the region considered, there may be one or two annual increments deposited, and an inappropriate count may lead to an error in the age estimation (Panfili *et al.*, 2002). The present study indicated an annual periodicity, with the deposit of a translucent chromophilic zone starting at the end of the WD season (May) and continuing during the WW season (June to September), with a peak of complete formation at the begin-

ning of the WW season (June to July). This result agrees with studies performed in sub-tropical countries (Grammer *et al.*, 2012; Chifamba and Videler, 2014), but not findings from tropical countries, which have indicated a biannual formation (Admassu and Casselman, 2000; Bwanika *et al.*, 2007; Gómez-Márquez *et al.*, 2008). The difference in the period of the annual deposit is not surprising. Translucent zone in reflected light (Admassu and Casselman, 2000; Panfili *et al.*, 2002), or opaque zone in transmitted light (Panfili *et al.*, 2002; Bwanika *et al.*, 2007), is known to correspond to a period of slow growth, which can be due to several factors, such as spawning activity, seasonal fluctuation in water temperature or in the quality and quantity of the available food (Yosef and Casselman, 1995; Panfili *et al.*, 2002). For *O. niloticus*, many studies have linked formation of the translucent zone to the spawning activity induced by rainfall (*e.g.* Duponchelle *et al.*, 1999; Admassu and Casselman, 2000;

Duponchelle and Legendre, 2000; Gómez-Márquez *et al.*, 2008). In the case of the NT2 Reservoir, although individuals are able to reproduce over the year, the reproductive peak occurs at the end of the dry season and the beginning of the warm and wet season in May-June. In this reservoir, juveniles of *O. niloticus* were recorded during the warm and wet season (June to October) and especially at the end in October (NTPC, unpubl. data). Thus, the timing of formation of the translucent zone in the present study could be attributed to slow somatic growth induced by reproductive activity, which occurs once at this time of the year. During the reproduction period, energy is allocated to gonad maturation for both sexes (Fryer and Iles, 1972; Jalabert and Zohar, 1982; Gómez-Márquez *et al.*, 2008). In addition, part of the energy is also allocated to reproductive behaviour. The male allocates energy to build and guard the spawning site, while the female ceases food consumption to incubate eggs and juveniles in its mouth (Gómez-Márquez *et al.*, 2008). The period of translucent zone formation observed in the present study agrees with the observations of Lowe-McConnell (1958) and Duponchelle and Legendre (2000), which indicate that the reproductive season of *O. niloticus* is influenced by latitude, stretching progressively from March to September between 15°N and 10°N and no longer limited to a single season below a latitude of 10°N.

The length-age key is a major element from the perspective of fisheries management. The analysis of the individual ages landed permits the determination of a potential risk of stock overexploitation. The length-age key was composed of 9 age-classes ranging from 0⁺ to 8⁺ years old, with a high variability in length for each age-class. Such variability has been present in some other studies on *O. niloticus*, even if it was not highlighted (Gómez-Márquez, 1998; Bwanika *et al.*, 2007; Gómez-Márquez *et al.*, 2008). This high variability could result from a long reproductive period over the

year, differential growth rates and the mixing of cohorts as reported by Jiménez-Badillo (2006) for *O. aureus* (Steindachner, 1864). A peak of reproduction existed between May and July, but some *O. niloticus* individuals of the NT2 Reservoir could reproduce between March and September, as juveniles have been observed in the NT2 Reservoir between March and October (M. Cottet, pers. comm.). This extended spawning period for *O. niloticus* has previously been reported (Lowe-McConnell, 1958; Duponchelle and Legendre, 2000). It is also possible that a limited number of captures in an age-group (7⁺ years, for example), due to the mesh-size used, induced an artificial variability in length for the given age-class because the variability decreases as the sample size increases (Frontier, 1983).

Mean length by age-class was lower than that found in other studies (Tab. III) in Africa (Admassu and Casselman, 2000; Bwanika *et al.*, 2007; Ouattara *et al.*, 2009), in America (Gómez-Márquez *et al.*, 2008; Novaes and Carvalho, 2012), and in Asia (Ishikawa *et al.*, 2013). This difference could be related to different parameters. First, it could be due to a heavy fishing regarding the population, as it was the case for the population at Lake Awassa (Casselman, pers. comm.). This difference could also be due to slower growth for the NT2 Reservoir *O. niloticus* population. Indeed, the present study found a growth rate of 0.08 year⁻¹, whereas the lowest value found in the meta-analysis conducted by Ishikawa *et al.* (2013) was 0.14 year⁻¹ for Lake Itasy, in Madagascar. Nevertheless, Gómez-Márquez (1998) reported very low growth (0.07 year⁻¹) for the *O. niloticus* of a Mexican lagoon, as the present study. It is common to observe growth variations between *O. niloticus* populations as a function of geographical region (tropical or subtropical countries), environmental factors (*e.g.* pH, water temperature, conductivity and nutrient availability), anthropic pressure (*e.g.* fishing effort) and the plasticity of the population

Table III. – Comparison of age and mean length of *Oreochromis niloticus* with previously reported studies in the world. Standard length (SL) and total length (TL).

Source	Geographic region	Type of ecosystem	Age group	Length (type of measurement, in mm)
Present study	Asia (Lao PDR)	Reservoir	1	105 (SL)
			2	165 (SL)
Admassu and Casselman (2000)	Africa (Ethiopia)	Lake	2	156 (TL)
Bwanika <i>et al.</i> (2007)	Africa (Uganda)	Lake	1	150 (TL)
			2	250 (TL)
Ouattara <i>et al.</i> (2009)	Africa (Côte d'Ivoire)	Reservoir	1	160 (TL)
			2	185 (TL)
Gómez-Márquez <i>et al.</i> (2008)	America (Mexico)	Lake	1	106 (SL)
			2	125 (SL)
Novaes and Carvalho (2012)	America (Brazil)	Reservoir	1	157 (SL)
			2	241 (SL)
Ishikawa <i>et al.</i> (2013)	Asia (Japan)	Estuary	1	138 (SL)
			2	202 (SL)

(Lowe-McConnell, 1958; Ishikawa *et al.*, 2013). Lowe-McConnell (1958) and Pullin (1988) attributed low growth of *O. niloticus* to poor diet. Thus, the low growth found for the NT2 Reservoir *O. niloticus* population could be attributed to food limitation. The NT2 Reservoir qualifies as an oligotrophic reservoir (Cottet and Visser, 2017) with a low production of chlorophyll *a* ($4.3 \mu\text{g}\cdot\text{L}^{-1}$) and low production of nutrients, with nitrate and phosphorus concentrations under the detection limit (Martinet *et al.*, 2016). Furthermore, the usual main food consumed by *O. niloticus*, namely cyanobacteria and diatoms (Figueredo and Giani, 2005), did not dominate the phytoplankton community of the NT2 Reservoir (Martinet *et al.*, 2016). It was mainly composed of Chlorophyta (Martinet *et al.*, 2016), a group in which some species cannot be digested and pass intact through the digestive tract of *O. niloticus* (Moriarty and Moriarty, 1973; Getachew and Fernando, 1989). Other parameters could be responsible for the slow growth of the *O. niloticus* population of the NT2 Reservoir; in the present study, it was only possible to conclude that this population grows more slowly than other populations in Africa, Central/South America and Sri Lanka in Asia.

The asymptotic length in the present study (658 mm) was higher than those of the populations of Lake Itasy in Madagascar (Ishikawa *et al.*, 2013) and Minnerya and Tabbowa reservoirs in Sri Lanka (Novaes and Carvalho, 2011; Ishikawa *et al.*, 2013), which were 572 and 411 mm, respectively. The higher value measured in the present study possibly arose from larger individuals present in our sample (up to 360 mm SL) than in previous studies for which large individuals ranged between 165 and 312 mm (SL) (Bwanika *et al.*, 2007; Gómez-Márquez *et al.*, 2008; Ouattara *et al.*, 2009; Novaes and Carvalho, 2012). This aspect of the size-class distribution has an influence on the von Bertalanffy growth function used to generate the value of the model.

The results of (i) sex ratio at the equilibrium, (ii) old age of some sampled individuals (7^+ and 8^+ years) and the high percentage of individuals landed with an age greater than 4^+ , (iii) the slow growth observed for this population, and finally, (iv) the probable late age of sexual maturity, tend to indicate that the population is not overexploited. The estimated age at sexual maturity should be interpreted with care due to the low quality of the data. Because the sampling strategy did not integrate the spawning zone, only a few mature females were caught, notably during the reproductive season. Indeed, *O. niloticus* reproduce in shallow water (Lowe-McConnell, 1958) where it is difficult to sample in the NT2 Reservoir, and the spawning sites were not clearly identified. The lack of knowledge or access to the spawning sites by fishermen could explain partly why the *O. niloticus* population is not overexploited. Limitation of access to spawners allows for stock renewal. However, a study should be conducted with fishermen to confirm this hypothesis. Furthermore, in the

context of limited access to spawners such as in the present study, it is possible that resting females were classified as immature. During adult life, gonads follow a maturity cycle (Pilling *et al.*, 2007), and not all females reach stages 3 to 5 at the same time of the year. Thus, females in stages 1 and 2 could have been overestimated in the present study because they were more accessible than mature females. For this reason, the SL_{50} and A_{50} given in the present study were only estimates and should be considered with caution. It may be interesting to determine if sexual maturity occurs later for the NT2 Reservoir population than for other studied populations. These data are of major importance for an exploited population in the context of fisheries management.

In the present study, both juveniles and females experienced isometric growth while males showed positive allometric growth. Some previous studies have reported positive allometric growth in Kenya and Saudi Arabia (Njiru *et al.*, 2006; Mortuza and Al-Misned, 2013), whereas other studies have indicated negative allometric growth for *O. niloticus* in Mexico, Brazil and Nigeria (Gómez-Márquez *et al.*, 2008; Novaes and Carvalho, 2012; Musa *et al.*, 2016) or isometric growth in Brazil (Barbieri *et al.*, 2000). Growth variation among *O. niloticus* populations is mainly explained by differences in environmental conditions, fish condition, local anthropogenic pressure and by the high plasticity regarding growth exhibited by *O. niloticus* (Melard, 1986). Furthermore, negative allometric growth was found only in studies where the *O. niloticus* populations were overfished (Gómez-Márquez *et al.*, 2008; Novaes and Carvalho, 2012) or where the environmental conditions were unfavourable (Musa *et al.*, 2016). Thus, the isometric and positive allometric growth found in the NT2 Reservoir indicated that the environmental conditions were acceptable for the *O. niloticus* population.

CONCLUSIONS

The present study highlights biological traits shared by the *Oreochromis niloticus* population from the Nam Theun 2 Reservoir with other populations from other ecosystems and geo-regions: formation of an annual annulus and isometric or positive allometric growth. However, specific biological traits (slow growth rate and a specific age-length key) are also evident. Finally, our results suggest that the *O. niloticus* population of the NT2 Reservoir was not overexploited at the time of the survey. However, a study focusing on age estimation at sexual maturity is required, along with population monitoring to observe the evolution of fishing effort and prevent potential over-exploitation in the long-term. A complete assessment of the status of exploitation of this species in the NT2 Reservoir also requires investigations of the total mortality rate, fishing mortality rate, rate of exploitation and critical length ratio. It is important to keep in mind that

O. niloticus in Lao PDR is an exotic invasive species. It may be more profitable and responsible to focus on native species and their potential regarding the fisheries with the goal of reservoir development in this country.

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